Regular paper

Acclimation response of spring wheat in a free-air CO$_2$ enrichment (FACE) atmosphere with variable soil nitrogen regimes. 3. Canopy architecture and gas exchange *

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Abstract

The response of whole-canopy net CO$_2$ exchange rate (CER) and canopy architecture to CO$_2$ enrichment and N stress during 1996 and 1997 for open-field-grown wheat ecosystem (*Triticum aestivum* L. cv. Yecora Rojo) are described. Every Control (C) and FACE (F) CO$_2$ treatment (defined as ambient and ambient +200 μmol mol^{-1}, respectively) contained a Low- and High-N treatment. Low-N treatments constituted initial soil content amended with supplemental nitrogen applied at a rate of 70 kg N ha^{-1} (1996) and 15 kg N ha^{-1} (1997), whereas High-N treatments were supplemented with 350 kg N ha^{-1} (1996 and 1997). Elevated CO$_2$ enhanced season-long carbon accumulation by 8% and 16% under Low-N and High-N, respectively. N-stress reduced season-long carbon accumulation 14% under ambient CO$_2$, but by as much as 22% under CO$_2$ enrichment. Averaging both years, green plant area index (GPAI) peaked approximately 76 days after planting at 7.13 for FH, 6.00 for CH, 3.89 for FL, and 3.89 for CL treatments. Leaf tip angle distribution (LTA) indicated that Low-N canopies were more erectophile than those of High-N canopies: 48° for FH, 52° for CH, and 58° for both FL and CL treatments. Temporal trends in canopy greenness indicated a decrease in leaf chlorophyll content from the flag to flag-2 leaves of 25% for FH, 28% for CH, 17% for CL, and 33% for FL during 1997. These results indicate that significant modifications of canopy architecture occurs in response to both CO$_2$ and N-stress. Optimization of canopy architecture may serve as a mechanism to diminish CO$_2$ and N-stress effects on CER.

Abbreviations: FH – CO$_2$-enriched, High-N; FL – CO$_2$-enriched, Low-N; CH – Control-CO$_2$, High-N; CL – Control-CO$_2$, Low-N; FACE – Free-air CO$_2$ enrichment; GLAI – green leaf area index; GPAI – green plant area index; LAI – leaf area index; LTA – mean leaf tip angle; PAR – photosynthetically active radiation; CER – whole-canopy net CO$_2$ exchange rate

Inroduction

Potential whole-canopy net CO$_2$ exchange rate (CER) is influenced primarily by the amount of photosyn-

thetically active radiation (PAR) absorbed (Gutschick 1991). Numerous investigations pertaining to the effects of increased atmospheric CO$_2$ on a wide range of plant species have been conducted and generally indicate that biomass accumulation rate and, therefore, LAI are increased, in some cases as much as 30% (Kimball

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1983; Idso and Idso 1994). Such structural changes in canopy architecture may influence the amount of PAR absorbed and, therefore, alter CER. Few studies have examined the effects of increasing atmospheric CO_2 and/or N-stress on agricultural food crops grown under field conditions and thus potentially fail to address modification of canopy N allocation and architecture due to increased carbon assimilation rate; therefore, greenhouse, potted plant, or measurements made at the organ scale may not reflect field results if canopy architecture were to be modified through increased carbon gain in response to rising CO_2. Furthermore, leaf assimilation rates are typically expressed on a leaf area basis whereas canopy photosynthesis and yield are represented in terms of ground area, making comparison between different measurement types difficult.

Since atmospheric CO_2 concentration is predicted to double in the next 50–100 years (IPCC 1996) and global wheat production exceeded that of all other small grain crops, yielding 613 million tons of grain during 1997 (U.N.–F.A.O. 1998), it is imperative that the effects of atmospheric CO_2 on field grown wheat are understood. Nitrogen availability is key to chlorophyll synthesis and therefore also related to canopy light capturing ability. Fertilization is not a viable option for many growers, particularly those existing at the subsistence level. The Maricopa, AZ FACE project provided a unique opportunity to study the canopy photosynthesis and architecture of field grown wheat exposed to CO_2 enriched (ambient $+200 \, \mu\text{mol mol}^{-1}$) and N-stress.

Wheat utilizes the C_3 photosynthetic pathway. When measured across an increasing range of CO_2 concentrations, the photosynthesis rate for C_3 plants will increase in a hyperbolic manner (Zelitch 1971; Idso and Idso 1994) until it becomes rate limited by the regeneration rate of ribulose-1,5-bisphophate and other biochemical factors at an atmospheric CO_2 concentration of $\sim 1000 \, \mu\text{mol mol}^{-1}$ (Sage 1994). As such, increasing atmospheric CO_2 is thought to increase carbon accumulation and growth (Chen et al. 1995; Poorter et al. 1997) and has been well demonstrated for pot-, chamber- and glasshouse-grown wheat (McKee and Woodward 1994; Smart et al. 1994).

Hocking and Meyer (1991) reported that plant height, tiller number, leaf area, dry matter and N content all increase significantly when wheat is grown in pots at both CO_2 enriched and $CO_2 \times$ N-stressed conditions. This suggests that for open field-grown wheat, canopy architecture may be dramatically altered through CO_2 induced-increases and N-stress-induced reductions in leaf area index (LAI). Canopy architecture has been demonstrated to play a significant role in light capture ability and canopy photosynthesis rate (Puckridge 1971; Johnson et al. 1981; Myneni et al. 1986). In fact, LAI is often used to estimate potential canopy photosynthesis and crop growth (Puckridge and Ratkowsky 1971; Goudriaan and Monteith 1990). These approaches reason that captured radiation will be converted at a given efficiency for carbon fixation, for which mean leaf angle distribution (LTA) has been demonstrated to be a key parameter (Richardson and Wiegand 1989). It would, therefore, be reasonable to assume that for $CO_2 \times$ N-stress experiments, a unique canopy architecture would develop for each treatment and that this architecture would influence canopy photosynthesis rate. This is, in part, supported by research conducted during the 1992–1994 $CO_2 \times H_2O$ stress (Garcia et al. 1998) which reported that CO_2 enrichment, when expressed on a leaf area basis, enhanced leaf photosynthetic rates by as much as 30% for wheat grown under non-stressed conditions, whereas respective final grain yields increased only 8–16% (Pinter et al. 1996a).

The objective of this experiment was to quantify changes in CER and alterations in canopy architecture in response to increased atmospheric CO_2 concentration and nitrogen stress. We hypothesize that an increase in atmospheric CO_2 concentration should result in increased CER. Furthermore, nitrogen stress will have a less significant impact upon CER at High-CO_2 than at ambient conditions. While we recognize that biochemical acclimation (see Adam et al. 2000 and Wall et al. 2000) and microclimate will influence the photosynthetic responses of wheat to N-stress and CO_2, we also hypothesize that CER will be dependant upon canopy architecture as measured by LAI, LTA, and leaf greenness within the canopy. In turn, a modified canopy architecture may potentially act as a compensation mechanism thereby reducing the relative effects of CO_2 and N treatments for CER when compared with photosynthesis rates reported for the individual leaves.

Materials and methods

Crop culture, CO_2 treatment, N treatment

A detailed description of crop culture and treatment

administration can be found in Kimball et al. (1999). In brief, this experiment was conducted at the Maricopa Agricultural Center, located in Maricopa, Arizona (33.30 N, 112.10 W) where wheat, *Triticum aestevum* L. cv Yecora Rojo, was grown in an open field. CO_2 enrichment was achieved using the *Free-Air CO_2 Enrichment* method (FACE) (Hendrey 1993; Wall and Kimball 1993; Hendrey and Kimball 1994; Kimball et al. 1995; Pinter et al. 1996b) and nitrogen fertilizer was delivered to each plot via subsurface drip irrigation. Control treatments were exposed continuously to ambient CO_2, ~ 370 μmol mol^{-1}, whereas CO_2 enriched treatments (FACE) received ambient $+200$ μmol mol$^{-1}CO_2$. High-N treatments received N at a rate of 350 kg N ha^{-1} during both experimental years, whereas the Low-N treatments received 70 kg N ha^{-1} during 1996 and adjusted to 15 kg N ha^{-1} during 1997 to allow for mineralization. Possible treatment combinations were therefore Control, High-N (CH); Control, Low-N (CL); FACE (CO_2 enriched), High-N (FH); and FACE, Low-N (FL) for each of the four replicates.

Measurement of CER

Open-type chamber systems (similar to those in Garcia et al. 1990) were used to collect canopy carbon exchange data. Limited resources allowed for the construction and implementation of only two complete paired sets of chambers and accompanying instrumentation, or enough to measure one replicate at a time. Each system was composed of centralized instrumentation and two chambers, each 1.00 m wide (spanning 4 rows and 2 sub-surface irrigation tubes), 0.75 m long, and 1.30 m tall. Air movement through the chamber was measured using a flow meter (Model 900, Sierra Instruments, Monterey, California)[1]. Using control signals sent from a datalogger (Model CR7, Campbell Scientific, Logan, Utah) to a set of solenoid valves that comprised a flow control device, gas flow from one of the chambers in each pair was directed to a pair of infra-red gas analyzers [(IRGA), Model LI-6262, LI-COR, Lincoln, Nebraska]. One IRGA set in absolute mode constantly monitored the CO_2 concentration entering a chamber and transmitted this data using a millivolt signal to the CR7. In turn, 10 s averages of this signal were provided as a reference gas concentration to a similar IRGA operating

in differential mode, which measured the differential CO_2 concentrations between the chamber inlet and outlet. Canopy photosynthesis was measured in this way for a period of 48–96 h. Chambers were then moved to a new replicate at the end of each measurement period.

Hourly averages were computed for each treatment and used to plot dawn-to-dusk CER curves. To calculate daily total carbon accumulation, CER was integrated between sunrise and sunset and plotted for all measurement days. Additionally, a spline-fitted curve was used to determine seasonally integrated carbon uptake between 50% emergence and 25% fractional absorbed PAR, for each treatment. The area under each curve was used to determine the seasonal integrated net carbon uptake during 1997. A trapezoidal integration routine, *Area × fm*, was used to perform these integrations (Sigma Plot, v. 4.01, SPSS Inc., Chicago, Illinois).

Leaf greenness, green plant area index, and leaf tip angle

Leaf greenness measurements were made to estimate chlorophyll content (Wood et al. 1993; Blackmer and Schepers 1995). Wheat canopies were visually distributed into three different height cohorts defined as uppermost fully expanded leaf, uppermost fully expanded leaf-1, and uppermost fully expanded leaf-2. Canopy greenness was measured at the distal, medial, and proximal adaxial surface of 5 leaves at each height cohort for each of the four rows enclosed by a chamber using a portable chlorophyll meter (Model SPAD 502, Minolta, Japan). LTA was measured under diffuse radiation conditions just prior to sunset on still days using a plant canopy analyzer (Welles and Norman 1991; Model LI-2000, Li-Cor Inc., Lincoln, Nebraska). These measurements were made on intact canopies located in both the area enclosed by chambers and in protected final harvest areas in all four replicates.

Plants were destructively harvested in all four replicates and separated into leaves, stems and crowns on a weekly basis during both growing seasons and used to determine the Zadoks growth stage (Zadoks et al. 1974), green leaf area index (GLAI), and green stem area index (GSAI). The GLAI and GSAI were added together to yield GPAI. An ANOVA was completed for GPAI using a general linear model (SAS 1990) for a strip-split plot experimental design.

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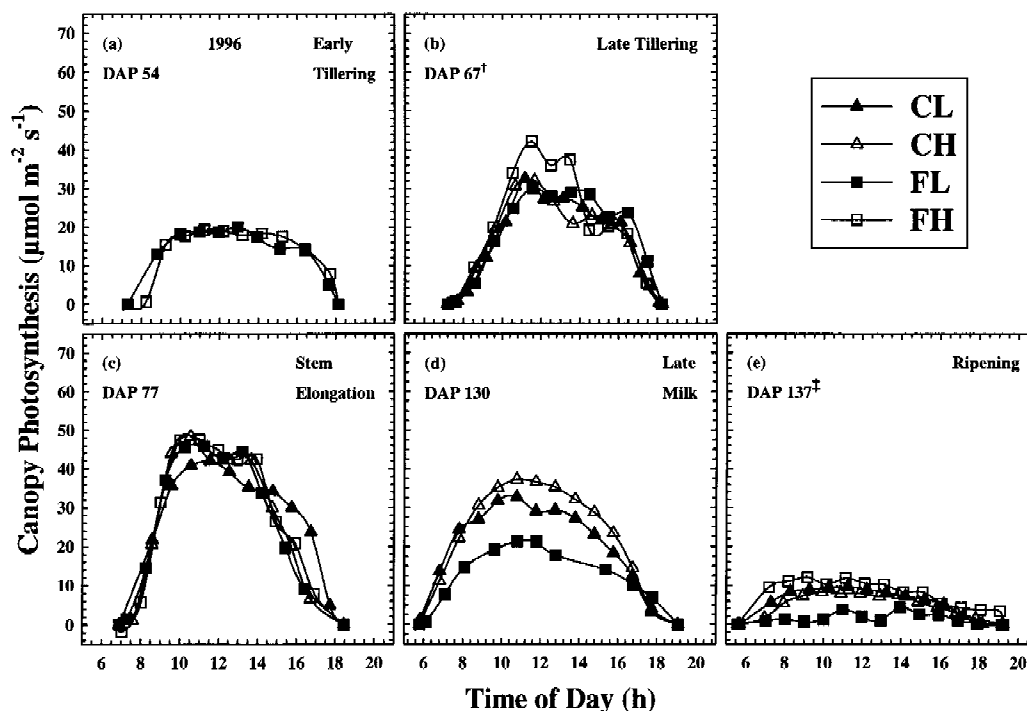
Figure 1. Dawn-to-dusk trends in whole-canopy photosynthesis during 1995–1996. Values reflect hourly averages for ambient CO_2, Low-N (CL), ambient CO_2, High-N (CH), ambient CO_2 + 200 μmol CO_2 mol^{-1}, Low–N (FL) and ambient CO_2 + 200 μmol CO_2 mol^{-1}, High-N (FH) treatments for the given days after planting (DAP) and growth stages. A value of 0 μmol M^{-2} s^{-1} was used at dawn and dusk. [†]FL data collected on DAP 65. [‡]FL and CL data collected on DAP 131 and 130, respectively.

Results

Atmospheric and edaphic factors

Selected days on which whole-canopy photosynthesis was determined had clear skies and adequate PAR. Meteorological data indicate that temperature, vapor pressure deficit, and solar radiation were similar for comparable data collection dates for 1996 and 1997. From planting to harvest, during both growing seasons, the total solar radiation increased two-fold from 14 to 28 MJ m^{-2} d^{-1}. Consequently, a corresponding increase in maximum air temperature from 18 to 34 °C occurred. Vapor pressure deficit ranged from 1 kPa to 5 kPa during the same time period. Phenological development was recorded using the average Zadoks numerical decimal code which was used to group whole-canopy gas exchange measurements into general growth phases (Zadoks et al. 1974).

Whole-canopy net photosynthesis rate

CER responded to elevated CO_2 and soil nitrogen treatment although the extent of any response was dependent upon time of day (light level) and growth stage. Therefore, the effects of CO_2 and N treatment on CER are presented as: (a) hourly rates (dawn-to-dusk), (b) daily cumulative effects, and (c) seasonal effects.

Dawn-to-dusk curves for CER are plotted as hourly averages for both 1996 and 1997 (Figures 1 and 2, respectively). During the time periods lasting from dawn until approximately 2 h after sunrise and 2 h prior to sundown until dusk, CER changed rapidly with changing solar zenith angle. Therefore, treatment comparisons were made at mid-morning (10:00 h, MST; Mountain Standard Time), midday (13:00 h) and mid-afternoon (16:00 h). Treatment effects were greatest at midday when PAR was greatest (Table 1), with the greatest enhancement of CER due to elevated CO_2 was greatest in 1997 at midday on DAP 36 and the least on DAP 137 in 1996. Low-N reduced CER the most during ripening for both years (-43% in 1996 and -69% in 1997). The magnitude of this effect was partially attributable to N-stress-induced accelerated senescence at the end of the growing season, reasoning that as nitrogen stress increased, remobilization of
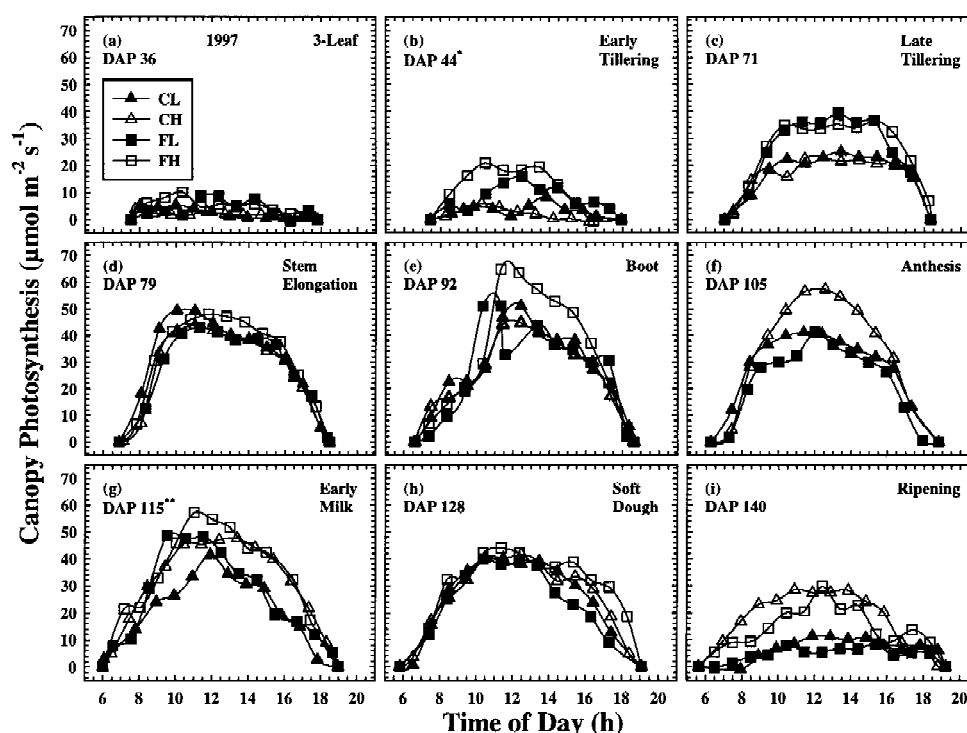
Figure 2. Dawn-to-dusk trends in whole-canopy photosynthesis during 1996–1997. [†]FL data collected on DAP 45. [‡]CL and CH data collected on DAP 119. Legend same as described in Figure 1.

nitrogen from leaves lower in the canopy occurred at a greater rate. Individual treatment effect combinations analyzed on a hourly basis, though inconclusive in and of themselves, were suggestive of a potential CO_2 by N-stress interaction.

The integrated values illustrated in Figure 3, like those determined on an hourly basis, are net values and reflect respiration as well as whole-canopy net carbon fixation. Admittedly, early season plant populations, though similar, were not numerically identical under each chamber. Therefore, variability in gas exchange rates was greatest at the beginning of the growing season and diminished with time as the canopy matured. Stimulation of CER by CO_2 enrichment was greatest during the 3-leaf and tillering growth stages during 1997 (250%). By canopy closure, when GPAI was approximately 3.0 (DAP 057), this stimulation was greatly diminished. The CO_2 effect gradually magnified during both years for the remainder of the growth stages, somewhat stabilizing during anthesis and ripening, but never regaining the significance noted during tillering.

Likely due to residual soil nitrogen content, as measured during November 1995, the effect of Low-N on CER were not observed in 1996 until approximately DAP 066. Analysis of the time of onset for of N-stress effects on CER for any particular Zadoks growth stage indicated that the onset of N-stress occurred earlier in 1997 and was detectable by DAP 051. N-stress effects on CER generally increased with growth stage, likely due to depletion of soil nitrogen resources.

Averaging over both years and both levels of N, CO_2 enrichment stimulated CER at mid-morning, midday, and mid-afternoon by 8%, 16%, and 5%, respectively; while N-stress, averaged over both CO_2 levels, inhibited CER during the same time intervals by 21%, 16% and 21%. In the High-N plots, the FACE treatment stimulated CER on a seasonal basis by 67% at mid-morning, 98% at midday, and 27% at mid-afternoon compared with an enhancement of −2%, 43% and 41% for the Low-N plots during the same time period. Within a CO_2 treatment, Low-N reduced CER by −4%, 3%, and 8% in the ambient plots, compared with reductions of 23%, 20%, and 30% in the CO_2-enriched plots at mid-morning, midday, and mid-afternoon, respectively.

Table 1. Canopy photosynthesis (Pn) at mid-morning (10:00), midday (13:00) and mid-afternoon (16:00) MST, daily total carbon accumulated and green plant area index (GPAI) for 1996 and 1997. Time-of-day values reflect hourly averages, whereas daily total carbon accumulated represent dawn-to-dusk integrations for ambient CO_2, N-stressed (CL), ambient CO_2, ample-N (CH), ambient CO_2 + 200 μmol CO_2 mol^{-1}, N-stressed (FL) and ambient CO_2 + 200 μmol CO_2 mol^{-1}, ample-N (FH) treatments for days after planting (DAP) and corresponding growth stages (common and Zadoks number). GPAI is the sum of the green stem and green leaf area determined through destructive harvest measurements

| Growth stage (Common) | Growth stage (Zadoks) | | DAP | | Treatment | Time of day (h) Canopy Pn (μmol m^{-2} s^{-1}) | | | | | |
| | | | | | | 10:00 | | 13:00 | | 16:00 | |
	1996	1997	1996	1997		1996	1997	1996	1997	1996	1997
3-Leaf		13.7		36	CL		5.4		1.3		0.2
					CH		1.8		2.0		1.5
					FL		2.5		6.8		1.1
					FH		9.2		5.4		2.9
Tillering (Early)	23.2	21.2	54	44	CL		4.6		4.9		3.3
					CH		4.8		2.3		0.0
					FL	18.2	4.9	20.1	15.8	14.2	5.9
					FH	16.6	16.2	17.9	18.4	16.0	0.0
Tillering (Late)	27.4	29.0	67	71	CL	21.3	20.2	27.4	24.1	21.3	21.7
					CH	25.3	17.3	23.8	22.3	18.3	20.9
					FL	20.7	29.0	28.5	37.7	23.3	30.7
					FH	26.9	31.0	36.8	34.6	19.3	34.8
Stem Elongation	33.0	31.1	77	79	CL	38. 2	41.8	37.2	39.4	26.8	30.3
					CH	46.2	49.4	42.2	40.3	13.2	31.1
					FL	45.6	40.8	44.5	38.5	14.5	30.7
					FH	47.5	41.6	42.3	47.1	20.8	37.6
Boot		44.5		92	CL		25.0		43.0		31.3
					CH		25.3		46.0		32.7
					FL		35.0		38.3		32.2
					FH		25.0		60.4		42.9
Anthesis		60.9		105	CL	38.3		39.2		29.8	
					CH		44.8		55.9		36.3
					FL		30.2		36.4		26.4
					FH						
Early Milk		71.4		118	CL		26.3		34.4		19.2
					CH		41.3		47.3		35.7
				115	FL		48.0		38.4		18.0
					FH		46.0		51.7		37.5
Soft Dough	81.0	83.5	130	128	CL	31.7	37.9	29.3	38.6	18.3	27.4
					CH	35.1	36.3	35.2	40.1	23.4	31.1
					FL	20.3	36.9	17.7	38.3	12.0	20.9
					FH		37.4		39.8		35.4
Ripening	84.8	87.2	137	140	CL	9.2	6.9	8.5	11.1	5.8	8.1
					CH	8.2	24.5	7.2	27.7	4.3	20.1
					FL	1.3	6.1	1.1	6.1	2.5	6.4
					FH	10.3	17.1	10.2	25.6	5.3	11.0
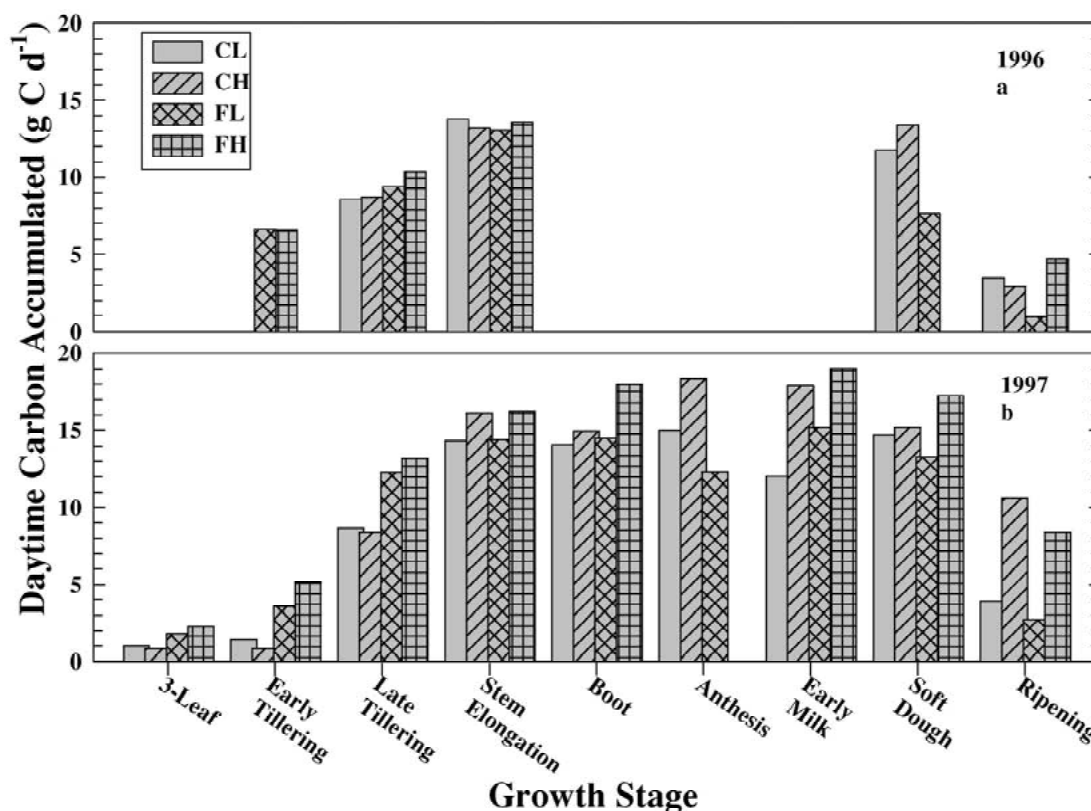
Figure 3. Daily total carbon uptake (net) for 1995–1996 and 1996–1997. Legend same as described in Figure 1.

Seasonal total carbon accumulated in kg C m^{-2} yr^{-1} were: 1.03 for CL, 1.20 for CH, 1.12 for FL, and 1.43 for FH. This represents a 13% seasonal enhancement of CER due to CO_2 enrichment over both N treatments and a reduction of 18% due to N-stress across both CO_2 treatments. Elevated CO_2 increased integrated CER by 16% at High-N but only 8% for the Low-N. Comparing the CH with CL, a 14% reduction in total seasonal carbon accumulation occurred due to N-stress, whereas a 22% reduction was evidenced for CO_2-enriched treatments.

Canopy architecture

The Low-N treatments experienced large reductions in GPAI at both levels of CO_2 (Figure 4) during most of both seasons (Table 2), whereas the FACE treatment tended to cause modest increases in GPAI. The GPAI reached maximums of 4.0, 6.0, 4.5, and 6.5 during 1996 for the CL, CH, FL, and FH treatments, respectively (Table 1 and Figure 4a). Likewise, the values for 1997 were 3.4, 5.4, 3.0, and 6.4 (Table 1 and Figure 4b). Seasonal analysis indicated that GPAI

was stimulated in FACE plots by 5% and reduced by 32% for Low-N treatments across both years. In the High-N plots, the FACE treatment was stimulated by 11% during the same time period, compared with a 4% reduction for the Low-N plots.

For 1996, early season LTA was variable and indeterminate due to small plant stature and rapid emergence of new leaves (Figure 5). However, temporal trends indicated that overall canopy architecture diverged significantly during stem elongation when canopy closure occurred. After canopy closure, Low-N canopies were erectile in nature and had a mean LTA of 58°. In contrast, CH canopies were more planar, developing a mean LTA of 52°. FH canopies were even more planar with a mean LTA of 48°. Spot measurements of LTA were performed during 1997 and confirmed the same general trends.

Canopy greenness

Temporal trends in canopy greenness, as estimated using a SPAD chlorophyll meter and collected during 1997 (Figure 6), indicate a mean difference in leaf

Table 2. Sources of variance in ANOVA for carbon dioxide (CO_2; Control compared to FACE), nitrogen [N; Low-N compared with High [7:35 g m^{-2} during 1995–1996 and 1.5:35 g m^{-2} during 1996–1997)] and replication (REP) effects on green plant area index (GPAI). ***, **, *, and ns for $P \leq 0.01$, $P \leq 0.05$, $P \leq 0.10$ and not significant, respectively

		1996						1997			
Date	DAP	Significance				Date	DAP	Significance			
		CO2 × N	REP	CO2	N			CO2 × N	REP	CO2	N
18 Jan.	34	ns	ns	**	ns	21 Jan.	37	ns	ns	ns	ns
30 Jan.	46	ns	ns	ns	ns	28 Jan.	44	ns	ns	ns	ns
						4 Feb.	51	ns	ns	ns	**
9 Feb.	56	ns	ns	ns	ns	11 Feb.	58	***	ns	ns	ns
19 Feb.	66	ns	ns	ns	ns	18 Feb.	65	ns	ns	ns	ns
						25 Feb.	72	ns	ns	*	ns
29 Feb.	76	ns	*	**	*	4 Mar.	79	ns	ns	ns	*
10 Mar.	86	ns	*	*	*	11 Mar.	86	*	*	*	***
20 Mar.	96	ns	**	**	*	18 Mar.	93	ns	*	ns	*
						25 Mar.	100	ns	**	ns	*
30 Mar.	106	ns	***	ns	*	1 Apr.	107	***	ns	ns	**
8 Apr.	115	ns	***	ns	*	8 Apr.	114	*	ns	ns	*
18 Apr.	125	ns	ns	ns	*	15 Apr.	121	ns	*	ns	*
						22 Apr.	128	***	ns	ns	*
26 Apr	133	*	ns	ns	*	29 Apr.	135	ns	ns	ns	*
6 May	143	ns	**	ns	*	8 May	144	***	*	**	ns

chlorophyll content when comparing the flag leaf to flag-2 of 25% for FH, 28% for CH, 17% for CL, and 33% for FL. These data suggest that while the High-N canopies were provided with luxury nitrogen, nitrogen stress was realized more rapidly in FL canopies when compared with CL. Nitrogen was applied in the High-N treatments just prior to anthesis (DAP 106), which resulted in the recovery of lower leaf greenness in FH and CH on day-of-year 092. The ratio of leaf greenness between flag and flag-2 for the time period lasting from tillering until senescence was maintained at 33% for FL, while CL dropped to 39% during the same time period. This suggests that sink demand for nitrogen was reached at a later point during the growing season due to lower CER (and thus reduced carbon accumulation) for CL when compared to FL. It is important to note that nitrogen levels were quite high in both the flag and the flag-1 leaves in the Low-N plants for much of the growing season.

Discussion

The rate at which a canopy intercepts radiation is closely related to crop growth and thus to CER (Porter 1989; Goudriaan and Monteith 1990). While replication is lacking in the canopy gas exchange data, trends appear suggestive both within a given day and seasonally for two distinct phases of growth: before and after canopy closure. It would be reasonable to expect that the greatest response of CER to CO_2 enrichment would occur during the stages of vegetative growth prior to canopy closure, as suggested by the data of Tischler et al. (1996) and Dijkstra et al. (1999), when intra-plant competition for light would be less than that which would be found in a mature canopy. This was also the case for this experiment, as CER responded the greatest to CO_2 enrichment when plants were small in stature. During the growth stages following canopy closure (stem elongation forward), maximum CER likely became increasingly light limited as a result of increasing LAI. For example, at the onset of the growing season, CO_2 had a substantial effect on seedling growth and enhanced canopy photosynthesis at midday in the High-N treatments (Table 1). This CO_2 effect rapidly diminished to approximately 30% during late tillering. While CER was apparently inhibited in the Low-N treatments during tillering, hourly N-stress effects became more pronounced with the progression of the growing season until canopy clos-
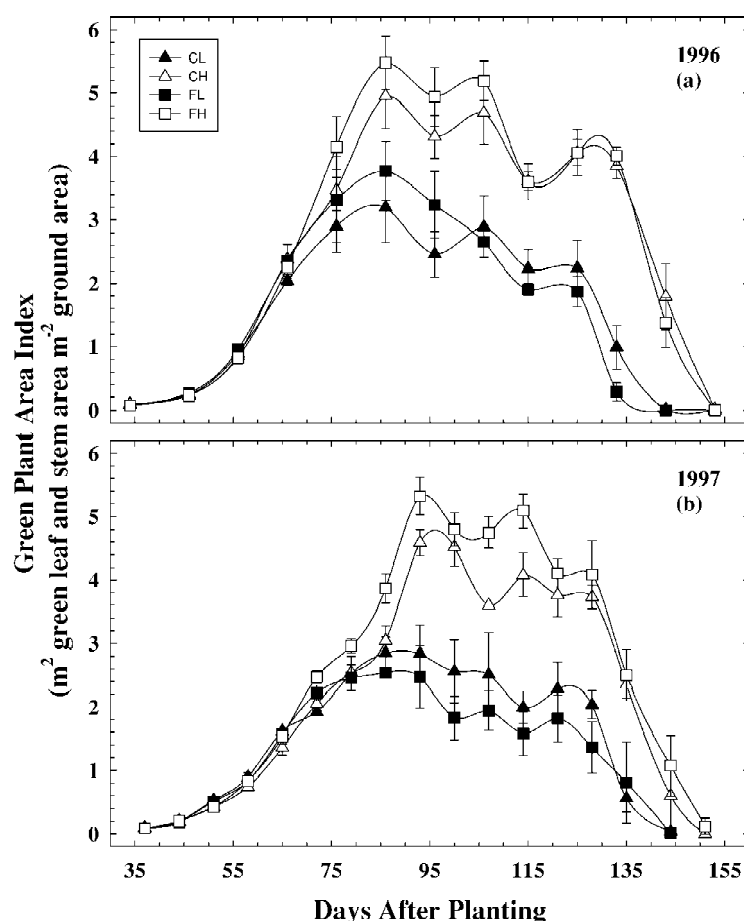
Figure 4. Temporal trends in green plant area index (GPAI) as calculated from weekly destructive harvest data during 1995–1996 and 1996–1997. Legend same as described in Figure 1.

ure (Figure 1), which is attributable to a decrease in available N coupled with increasing N-demand. This effect is also observed in daily total carbon accumulation (Figure 3). After canopy closure, the N-stress effect on CER was maintained at approximately 30% until ripening. These data suggest that the advantages conferred by CO_2 enrichment and the disadvantages by N-stress are diminished by canopy development.

For High-N treatments, it is reasonable to assume that the amount of light penetrating to leaves situated lower in the canopy was less than that of Low-N treatments because of increased GPAI caused by increased carbon gain. Thus, the effectiveness of lower leaves in contributing to CER was dependant upon GLAI. This effect was most significant for FH. Conversely, N-stressed treatments had significantly lower GPAI (Table 1 and Figure 4), indicating that light penetration to lower canopy leaves would occur to a greater
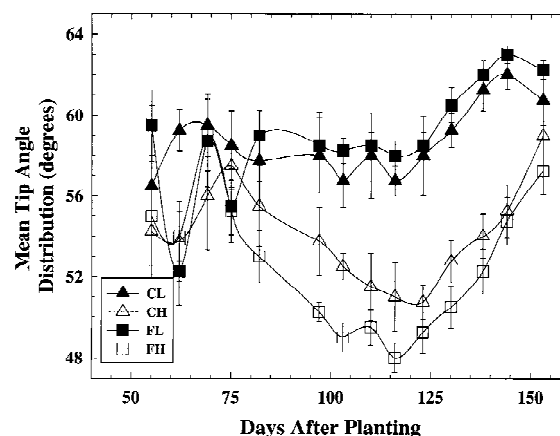
Figure 5. 1996 temporal trend in leaf tip angle (LTA) distribution. 90° represent a level surface. Legend same as described in Figure 1.
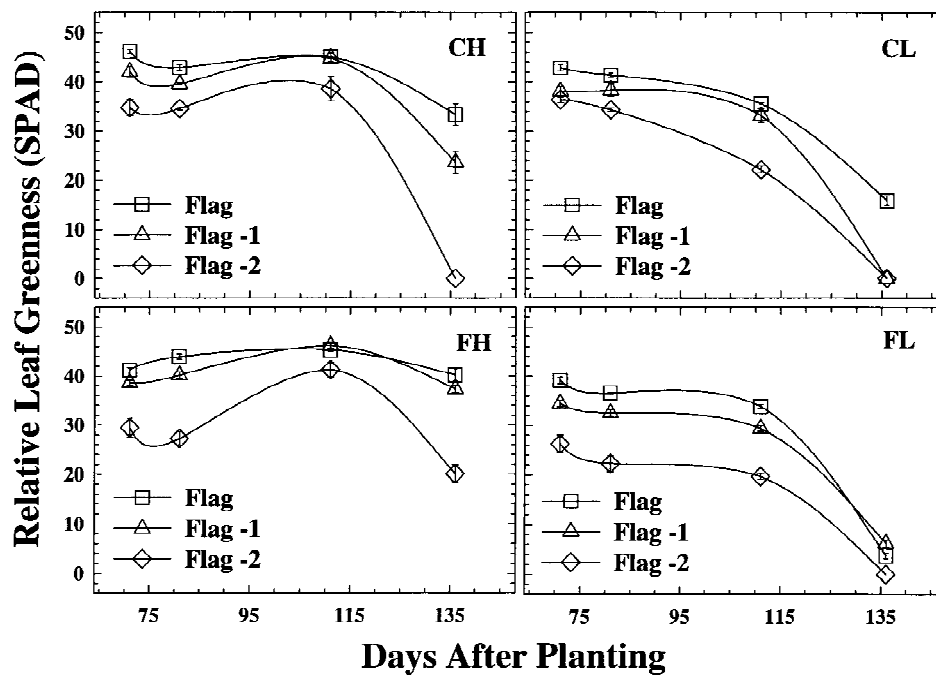
Figure 6. 1997 temporal trend in canopy greenness. Mainstem leaf greenness for flag, flag-1 (e.g., one leaf from the top), and flag-2 leaves as measured using a portable leaf chlorophyl meter. Legend same as described in Figure 1.

degree. These leaves were also the most erectophile. Therefore, solar radiation would be more uniformly distributed in Low-N treatments and potentially incident on a greater photosynthetically active leaf area by canopy depth. This is most easily demonstrated by expressing canopy gas exchange on a LAI basis as opposed to ground area. For example, were this to be done at 13:00 for DAP 115 in 1997, the resulting rates would be: 6.1, 12.5, 6.8, and 9.2 μmol m^{-2} (leaf area) s^{-1} for FH, FL, CH, and CL treatments, respectively. In general, as GPAI increases, CER per unit green leaf area decreases.

This effect would be magnified given the more erectile nature of N-stressed wheat canopies, as light capturing ability during early morning and late afternoon hours would be enhanced. In general, model evaluation of leaf angle and PAI indicate that photosynthetic efficiency is greatest at high leaf angle (Duncan 1971). This became somewhat more apparent when midday maximum canopy photosynthesis rates during boot, anthesis, and early milk stages of growth are compared with late afternoon rates. The average seasonal change from midday to afternoon for whole-canopy photosynthesis rate was approximately 49% for FH, 44% for CH, 42% for FL, and 36% for CL, indicating that elevated CO_2 maintained whole-canopy

photosynthesis rates at midday levels for a greater portion of the day. During the same time period, leaves were measured to be more erect in Low-N plots than those in the High-N.

Leaf N concentration, combined for all leaves in the canopy, was determined by Sinclair et al. (2000). For both experimental years, N concentration ranged from 50 to 60 mg g^{-1} 30 days after planting and gradually fell throughout the season for all treatment to 5–15 mg g^{-1}. During the latter vegetative stages (DAP 60) until the end of the season, High-N leaves had N contents ranging from 20–45% greater than those of the Low-N leaves. The canopy greenness measurements (Figure 6) illustrate that, whereas the High-N canopies were provided with adequate nitrogen, nitrogen stress was realized more rapidly in FL canopies because of higher canopy photosynthesis rates when compared with CL (Figure 6). Nitrogen was applied to the High-N treatments just prior to anthesis, which resulted in the recovery of lower leaf greenness in FH and CH on DAP 108 (Figure 6). The ratio of leaf greenness between flag and flag-2 was maintained at 33% for FL, while CL dropped to 39% during the same time period. This suggests that sink demand for nitrogen was reached at a later point during the growing season due to lower canopy pho-

tosynthesis rates when FL was compared with CL. It was also observed on a proportional basis that a significant amount of nitrogen was maintained in the Low-N treatment flag-1 leaves for the entire growing season. Hence, the allocation of nitrogen and thus chlorophyll, within the canopy in coordination with GPAI and LTA, tended to increase the effectiveness of the lower canopy. Lower canopy leaves in FL were greener in comparison to the flag leaf than those of CL suggesting that light capturing ability was increased and acted as a compensation mechanism which diminished overall N and CO_2 effects. The idea that canopy light capturing ability is improved at elevated CO_2 is in part supported by previous experimentation by Long and Drake (1991) and Osborne et al. (1998), who found that at the leaf level, quantum yield of photosynthesis is higher in shaded leaves.

By itself, current ambient CO_2 concentration rate limits canopy photosynthesis for C_3 plants. While biochemical acclimation with respect to leaf depth within a canopy (Osborne et al., 1998 and Adam et al. 2000) and microclimate most certainly play significant roles in the response of CER to CO_2 and N-stress, it can generally be speculated that with increasing stress, whether because of nitrogen or low CO_2, the efficiency of whole-canopy photosynthesis with respect to light capturing ability will increase. A similar response would not be apparent at the individual leaf level for this experiment because light was rarely limiting. In effect, the addition of biomass due to elevated CO_2 and High-N caused light to become a third treatment.

In conclusion, wheat CER was improved by CO_2 stimulation and reduced by N-stress. However, the morphological responses of intact wheat canopies, as manifested in stress driven changes in canopy structure, improved CER and likely partially compensated for the treatment effects apparent at the observed biochemical (Adam et al. 2000) and individual leaf levels (Wall et al. 2000). Without use of the FACE system, these observations could not have been made as similar greenhouse or pot-based studies would prove insufficient because they cannot adequately allow for natural development of canopy structure.

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